

DETECTION OF PALYNOLOGICAL INTROGRESSION IN *SALVIA* (LABIATAE)

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ABSTRACT: It has been proposed that *Salvia*, as it occurs in western North America, arose through post Pleistocene hybridization and introgression. For reason of a scanty fossil record, little is known of this postulated origin. Herein is presented a technique for detecting instances of introgression using essential features of pollen grains.

INTRODUCTION

Palynology is a relatively young discipline in Botany and many of the techniques for studying palynological problems have not yet been formulated. Herein I have presented an approach to the study of extant populations of *Salvia* based upon the use of palynological features and stressing size relationships. Pollen presents a variety of morphological features which may be used as taxonomic characteristics, just as flowers and foliar appendages have been used in the past. A palynological technique for surveying introgression as an evolutionary phenomenon in the absence of usable floral or vegetative material may prove to be a useful way to reconstruct the putative hybrid ancestry of certain plant genera such as *Salvia*. This work could presumably be extended to collections of fossil grains when there are sufficient numbers.

The genus *Salvia* as it occurs in southwest North America is grouped into section *Audibertia* which is comprised of 19 species forming a dominant element of the coastal sage community. This association represents a modern derivative of the Madro-Tertiary Geoflora. Although the presence of *Salvia* in this geoflora has been implied, no fossil records are known for vegetative material. However, *Salvia* leaves are less sclerophyllous than most of the other members of the association and are thus not as easily fossilized.

Chromosome numbers reported by Epling, Lewis, and Raven (1962) correlated with distribution records suggest that most members of section *Audibertia* are relatively young and probably arose through Pleistocene disruption creating new habitats which could be occupied by hybrid recombinants. The ability of hybrids thus formed to backcross to parental species could result in introgressed combinations more capable of existing in the newly-formed habitats than were their progenitors. It is obvious that the California species of *Salvia* have had common recent histories, for hybrids between species of di-

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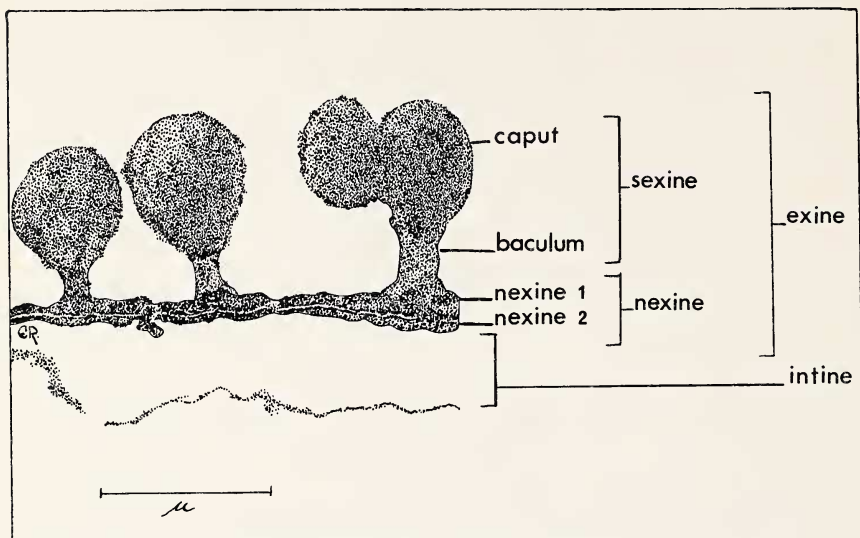


Figure 1. Pollen stratification after the terminology of Erdtman.

verse morphology are not uncommon in nature; furthermore, they often show a high degree of fertility and chromosomal homology. Backcrossing to one or both of the parental species in disturbed areas leads to hybrid swarms and in some cases introgression. Despite weak barriers to hybridization, the members of *Audibertia* maintain their genetic and morphological identity except in disturbed habitats. Usually these habitats are reconstituted in a few years and the parental species once more dominate the area. The hybrid habitat as discussed by Anderson (1948) is therefore a reality only in terms of a few generations. Even the site of Anderson and Anderson's famous *Salvia* study (1954) is no longer introgressed, for the disturbance which resulted from the planting of an olive orchard no longer exists, and the dense canopy of the olive trees has eliminated hybrids which were found "in and among the olives." (sic.)

MATERIALS AND METHODS

Eleven interspecific hybrids have been produced by hand pollinations in the greenhouses of San Fernando Valley State College in Northridge, California. A few of these are not found in nature as their ranges do not overlap or are not in such proximity as to permit pollinators to effect pollination. Most, however, do occur in nature and are to be found as F_1 hybrids. Introgression in nature has been documented for only three species in this section. The fertility of hybrids and backcrosses is rarely less than 50% and is sometimes as high as

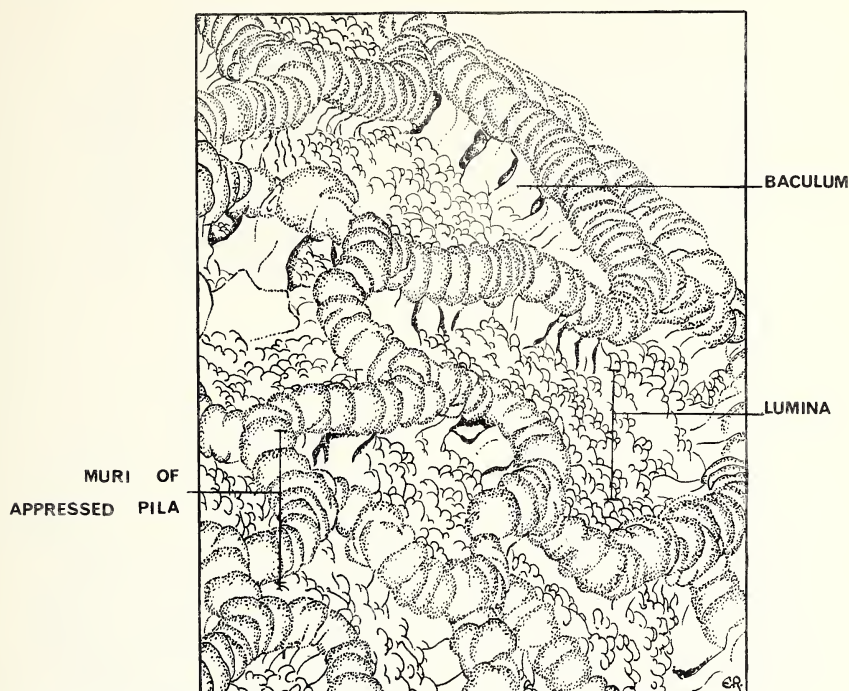


Figure 2. Reticulate stratification of the sexine of *Salvia*.

98%, as determined by staining pollen with lactophenol blue. Seed set seems normal but the number of viable seeds is less than 3%.

It has been ascertained by Emboden (1964) that species of *Audibertia* have pollen morphology which is sufficiently distinct to distinguish them one from another on the basis of size, shape and exine stratification. It was thought that the pattern of introgression might be studied by using scatter diagrams, which have been so useful in portraying introgression when morphological characters have been used. If this should prove accurate in portraying contemporary introgression, it would be important in establishing introgression as a factor in speciation where Post-Pleistocene fossil grains can be found in abundance.

The hexacolpate pollen of *Salvia* is distinct from other genera of the coastal sage community, and indeed from most pollen. This grain is thought to have arisen from the tricolpate condition through a protrusion of the thinner walls of the three colpi. Using the terminology of Erdtman (1958) (Figures 1 and 2), *Salvia* pollen may be described as medium to large, suboblate to prolate, having a reticulated exine of continuous or discontinuous muri which

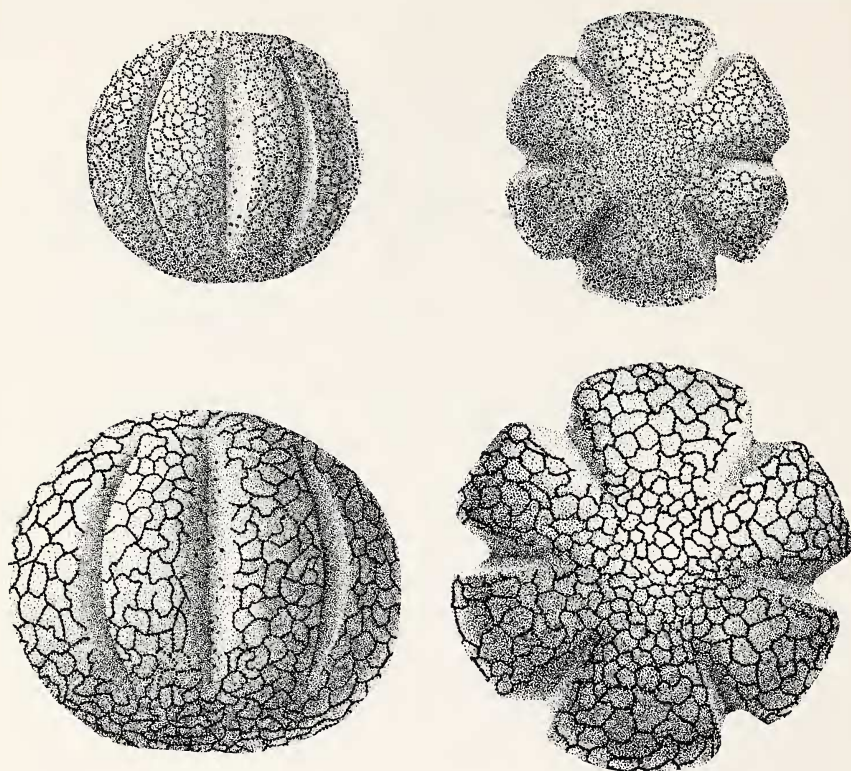


Figure 3. Pollen grains: upper—*Salvia mellifera*; lower—*S. apiana*. Polar, right column, and equatorial, left column, views.

may be intersected by muroid ridges or may contain a few isolated pila. (Figure 3.) This description of pollen of section *Audibertia* is consistent with Panelatti's (1960) characterization of pollen from Central and South America, and western Europe. It has been commonly observed that the size of contemporary and fossil pollen grains may vary with treatments; however Faegri and Deuse (1960) state, "... there are important pollen types within which a further taxonomic differentiation cannot be made by means of qualitative morphology, and where more or less successful attempts have been made to differentiate by means of size statistics." Inasmuch as pollen grains of the California *Salvias* exhibit size extremes that are often considerable, plotting polar axis against equatorial axis (ordinate and abscissa) might give a picture of hybridizing entities as distinct groupings, with hybrids as intermediates and backcrossing showing some sort of continuum between the F_1 individual and one of the parents. Such information might give insight into the origins of some of the

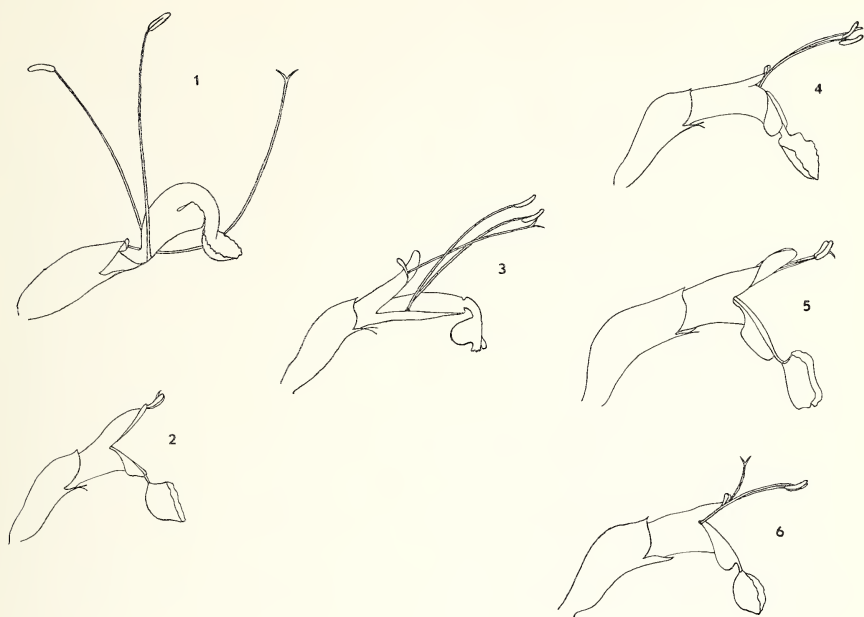


Figure 4. Flowers of *Salvia apiana*, *S. mellifera* and hybrids: 1. *S. apiana*; 2. *S. mellifera*; 3. F_1 hybrid; 4, 5, 6, introgressants.

species in this section. Miocene grains found on the Kenai Peninsula of Alaska compare favorably with those of a few relictual species of the present (Emboden, 1964).

Throughout coastal southern California, there are numerous areas in which the overlapping ranges of *S. mellifera* and *S. apiana* have resulted in the production of hybrids. Where major disturbances have been observed, hybrids and backcrosses generally are found. Such a site is in the San Gabriel Mountains above Arcadia. This is one of the two sites studied by Anderson and Anderson (1954). In contrast is a site in the Santa Susana Mountains three miles north of San Fernando Valley State College on Zelzah Avenue, Northridge, where populations of *S. apiana* and *S. mellifera* coexist in an area of about one square mile. The former occupies the steep well-drained slopes facing south and west, while the latter occupies a more mesic, north-facing ravine and the lower slopes. A single putative F_1 hybrid is known from this area.

Pollen grains were treated with lactophenol blue and allowed to remain in solution for 24 hours. Fifty grains were measured from each individual. This treatment introduces an increase in size of grains and is not comparable to grains treated by acetolysis and mounted in silicone oil. Specimens of the plants

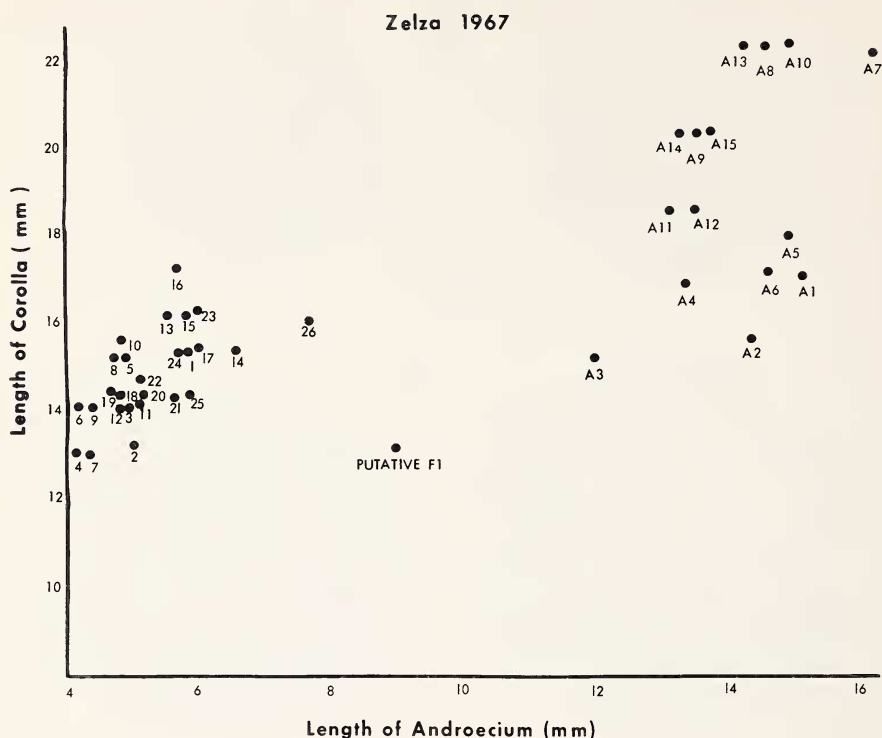


Figure 5. Scatter diagram of populations of *S. apiana* (upper right) and *S. mellifera* in the absence of introgression.

from which the pollen was taken are on deposit in the herbarium of San Fernando State College, Northridge, California.

RESULTS

Scatter diagrams based on floral characteristics of corolla length vs androecial length (characters found to be strongly correlated with other characters of the respective species) demonstrate that an introgressed population such as that in Arcadia is easily distinguished from populations which have no known history of introgression (Figures 5 and 6). When pollen of individuals from the Zelzah and Arcadia sites were compared on scatter diagrams using the polar and equatorial axes of the pollen grains as ordinate and abscissa, a similar phenomenon was observed (Figures 7 and 8). Introgression in the Arcadia population was manifest as conspicuous backcrosses to the F_1 hybrid and sub-

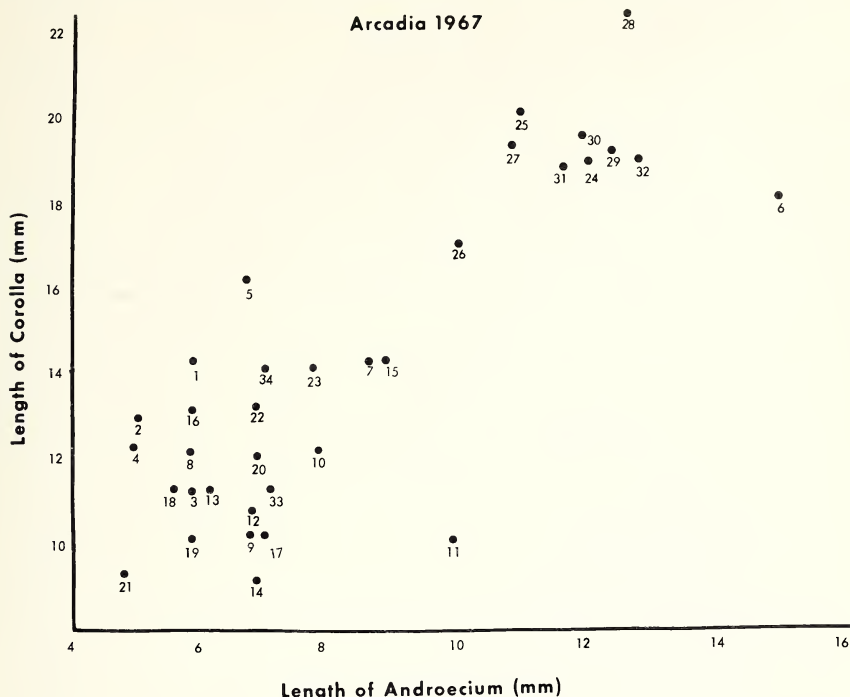


Figure 6. Scatter diagram of an introgressing population of *S. apiana* and *S. mellifera*.

sequent hybridization within the sub-mellifera population. The area occupied by *S. mellifera* individuals on the scatter diagram is considerably increased in the direction of *S. apiana*.

In both sets of scatter diagrams, a comparison of the position of individuals reveals an impressive correlation. That is, palynological evidence drawn from size relationships is able to portray introgression as clearly as morphological characters and is strongly correlated with them.

CONCLUSION

It would seem from the evidence presented, that the postulated post Pleistocene hybridization which gave rise to section *Audibertia* could be substantiated by a careful analysis of fossil *Salvia* pollen. It has already been established (Emboden, 1964) that both contemporary and fossil grains of *Salvia* can be identified on the basis of size and stratification differences. This new tool for analyzing palynological introgression would not only permit a depiction of hybridization, but would establish the role of introgression in evolu-

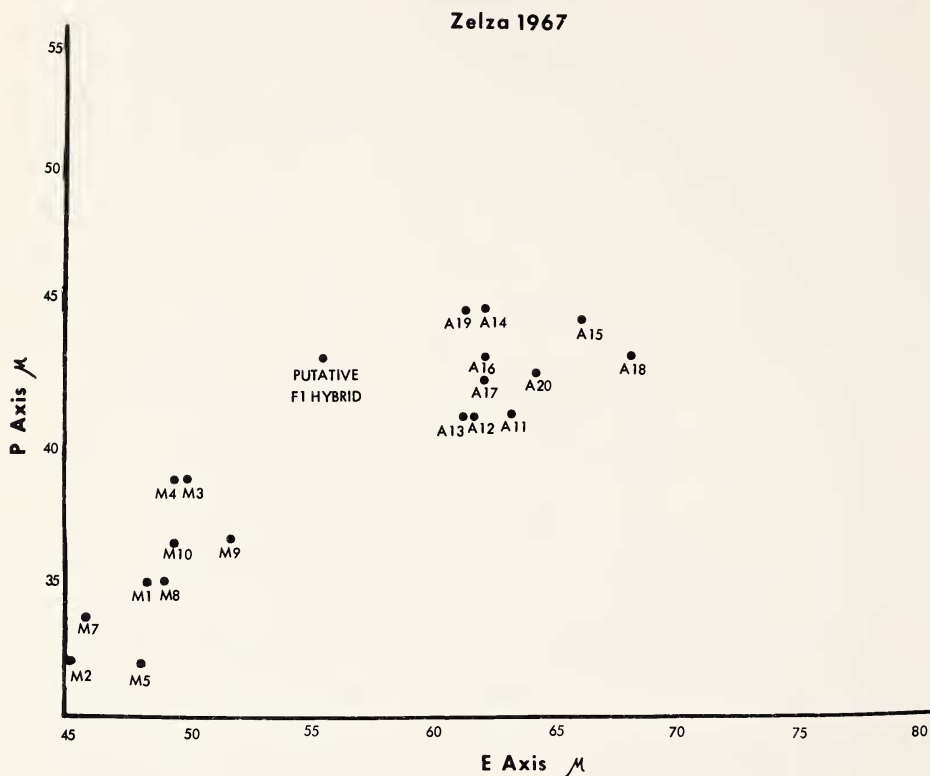


Figure 7. Populations of *S. apiana* and *S. mellifera* based on pollen measurements. Introgression is absent.

tion. An extensive collection of fossil *Salvia* pollen is not at this time available. When a number of these hexacolpate grains of two species can be taken from a single site, the application of this technique should prove most valuable. A knowledge of the origin of a dominant taxon of the coastal sage association would be a major contribution toward understanding the evolutionary processes by which the whole association came into being.

ACKNOWLEDGMENT

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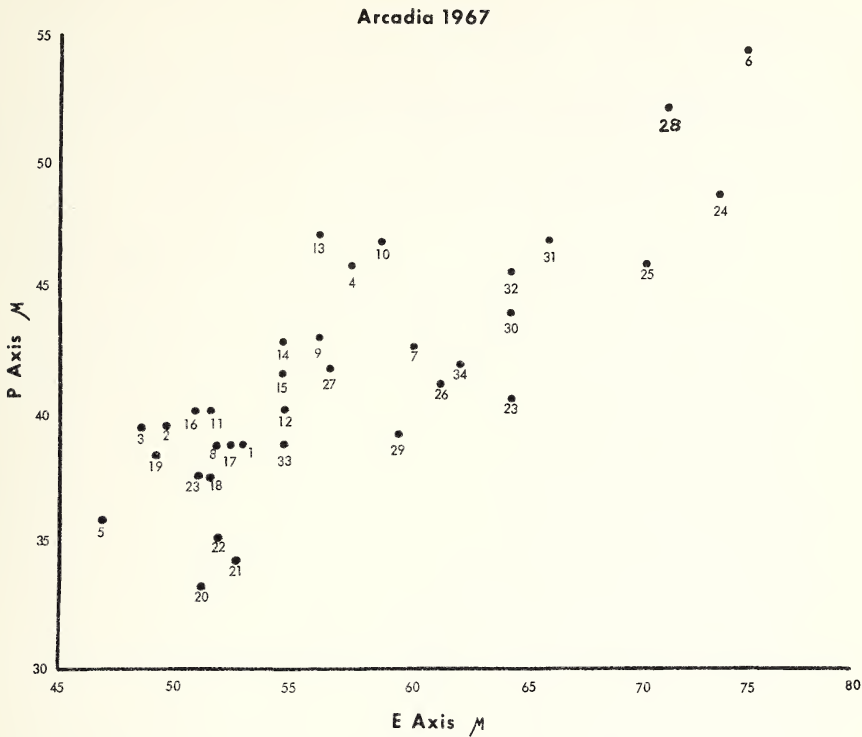


Figure 8. Palynological introgression between *S. apiana* and *S. mellifera*.

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